

**A new genus and species of frog from Bahia, Brazil (Amphibia:
Anura: Leptodactylidae) with comments on the zoogeography of the
Brazilian campos rupestres**

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Abstract.—A new genus and species of frog, *Rupirana cardosoi*, is described from the northern Espinhaço Range in the State of Bahia, Brazil. The new genus shares most character states with the genus *Thoropa*, but cladistic analysis of morphological data indicates that most of these shared features are primitive states. The cladistic analysis indicates that *Rupirana* and *Thoropa* do not have a close sister-group relationship with each other. *Rupirana cardosoi* is another addition to the many species endemic to the campos rupestres of the Espinhaço Range. The amphibians of the campos rupestres show a much stronger biogeographical affinity with the Atlantic Forest biota than other groups studied; these other groups show a much stronger affinity with the biota of the diagonal of open formations running from northeast Brazil (caatingas-cerrados) to Argentina and Paraguay (Gran Chaco).

Several years ago, Dr. Miguel T. Rodrigues brought my attention to a series of unusual frogs he had collected at two localities in the State of Bahia, Brazil, asking me if I knew what they were. I did not. Drs. Rodrigues and P. E. Vanzolini kindly put the specimens at my disposal for further study, but for various reasons, detailed study was delayed. Shortly after I had examined aspects of the myology and skeleton of the taxon, I had occasion to evaluate some of the problematical specimens of the Werner C. A. Bokermann collection as they were being catalogued into the Museu de Zoologia da Universidade de São Paulo collection. I found a series of the same taxon from a third locality in Bahia. All known localities are in the distinctive campos rupestres formation of Brazil. The purpose of this paper is to demonstrate that the new frog differs from all other known leptodactylid genera, provide a description for it, and briefly comment on its relationships and zoogeography.

Methods and Materials

One male (MZUSP 65204) was superficially dissected to obtain myological information on jaw, hyoid, and thigh musculature for the characters used in a previous study of leptodactylid relationships (Heyer 1975). A second female specimen (MZUSP 68959) was cleared-and-stained using the double-staining technique for cartilage and bone (Dingerkus & Uhler 1977) to evaluate osteological features.

For the species description, measurement data were taken with a dial calipers to the nearest 0.1 mm following the definitions in Heyer et al. (1990).

Relationships were analyzed with PAUP 3.1 (Swofford 1993).

Comparison with Leptodactylid Genera

Lynch (1971) still provides the most complete data set for leptodactylid genera, providing a baseline for comparison with subsequent studies. He recognized four New World subfamilies of the family Lep-

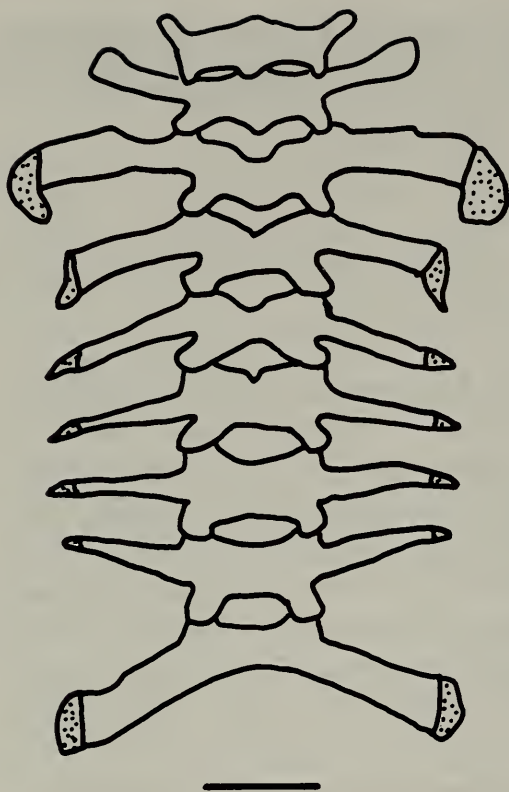


Fig. 1. Vertebral column of *Rupirana cardosoi*, MZUSP 68959. Cartilage stippled. Scale line = 2 mm.

toleptodactylidae: Ceratophryinae; Elosiinae; Leptodactylinae, and Telmatobiinae. The Australian and African leptodactylids Lynch treated as subfamilies of the family Leptodactylidae are now recognized as the separate families Myobatrachidae and Heleophrynidae, respectively (Frost 1985; Duellman & Trueb 1986).

The Bahia frog is not a member of the subfamilies Ceratophryinae, Elosiinae, or Leptodactylinae as defined by Lynch (1971). Rather than document this statement with a comparison of all states Lynch used, only a single character is used as an example. Ceratophryinae members have widely expanded transverse processes of the anterior presacral vertebrae; the Bahia frog does not (Fig. 1). Elosiinae species have a pair of dermal, scute-like glandular pads on the dorsal surface of each digital disk; the Bahia form lacks digital disks. Leptodactylinae genera have a bony sternal style; the sternum is a cartilaginous plate in the Bahia frog (Fig. 2).

Lynch (1971:112–113) listed nine char-

acters defining the subfamily Telmatobiinae (character numbers are those used by Lynch): (1) sternum cartilaginous; (2) vertebral shield lacking; (3) transverse processes of the anterior presacral vertebrae not widely expanded; (9) when present, maxillary teeth blunt and pedicellate; (35) mandible lacking odontoids; (39, the 38 is a typographical error on p. 113) *m. petrohyoideus anterior* and *m. sternohyoideus* insert on the lateral edge of hyoid plate; (48) eggs laid in water, in terrestrial situations, or in bromeliads. The egg deposition site is unknown for the Bahia frog; it agrees in the rest of the character states listed for the subfamily.

Lynch (1971) defined five tribes of Telmatobiinae and one genus he was unable to assign to any of these tribes: Alsodini; Eleutherodactylini; Grypiscini; Odontophrynini; Telmatobiini; and the genus *Scythrophrys*.

The Bahia frog cannot be assigned to the Eleutherodactylini, Grypiscini, Odontophrynini, Telmatobiini, or *Scythrophrys*. Again, for sake of brevity, only examples are used to document this statement. Members of the Eleutherodactylini have rounded sacral diapophyses and males lack cornified nuptial asperities; the Bahia frog has flattened sacral diapophyses and the males have cornified nuptial asperities. In species of the Grypiscini, the frontoparietal fontanelle is not exposed; in the Bahia frog it is (Fig. 3). Members of the Odontophrynini have short transverse processes of the posterior presacral vertebrae; the Bahia frog has long processes (Fig. 1). Members of the Telmatobiini have cervical cotyles that are narrowly separated with two distinct articular surfaces (Lynch's type II, 1971:54); the Bahia frog has widely spaced cervical cotyles with two distinct articular surfaces (Fig. 4, Lynch's type I, 1971:53). *Scythrophrys* has rounded sacral diapophyses and a concealed tympanum; the Bahia frog has flattened sacral diapophyses and an exposed, well-developed tympanum.

Lynch (1971:123–124) defined the Tribe

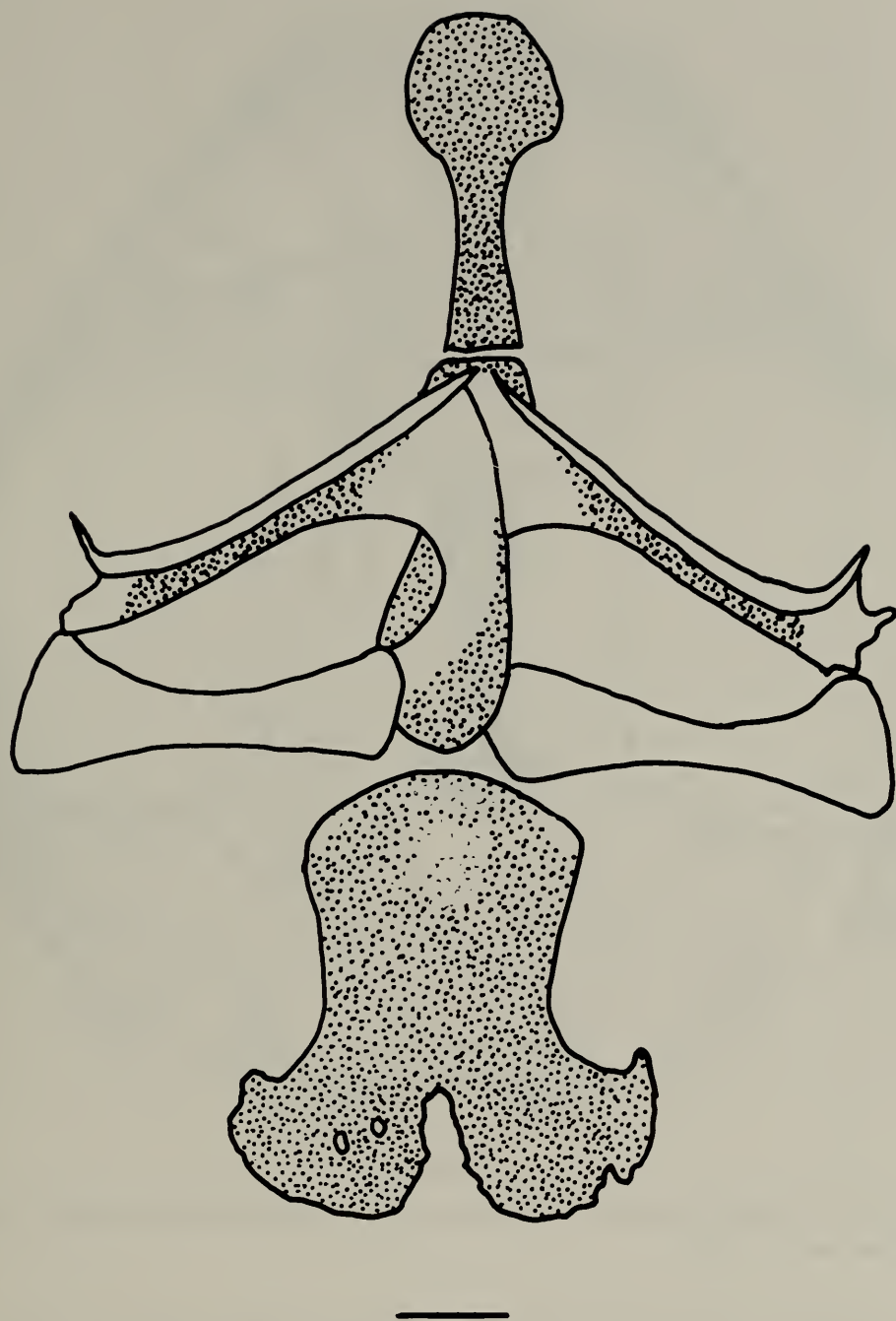


Fig. 2. Ventral portion of pectoral girdle of *Rupirana cardosoi*, MZUSP 68959. Cartilage stippled. Scale line = 1 mm.

Alsodini based on 16 characters (numbers are those of Lynch): (3) transverse processes of posterior presacral vertebrae long; (4) cervical cotylar arrangements type I or II; (5) cervical and second vertebrae not fused; (6) cranial bones not involved in dermos-tosis; (7) omosternum present, moderately large; (8) sacral diapophyses somewhat enlarged; (9) maxillary teeth blunt, pedicel-late; (12) facial lobe of maxilla deep, not exostosed; (17) nasals not in contact with

frontoparietals; (18) frontoparietal fontanelle exposed, moderate-sized; (19) frontopari-et al not fused with proötic; (21) temporal arcade lacking; (37) alary processes of hy-oid plate on narrow stalks; (42) male with cornified nuptial asperities on thumb; (45) outer metatarsal tubercle present, inner metatarsal tubercle normal; (46) larvae with median vent. Larvae are unknown for the Bahia frog. In all other characters, except (8), the Bahia frog matches exactly the def-

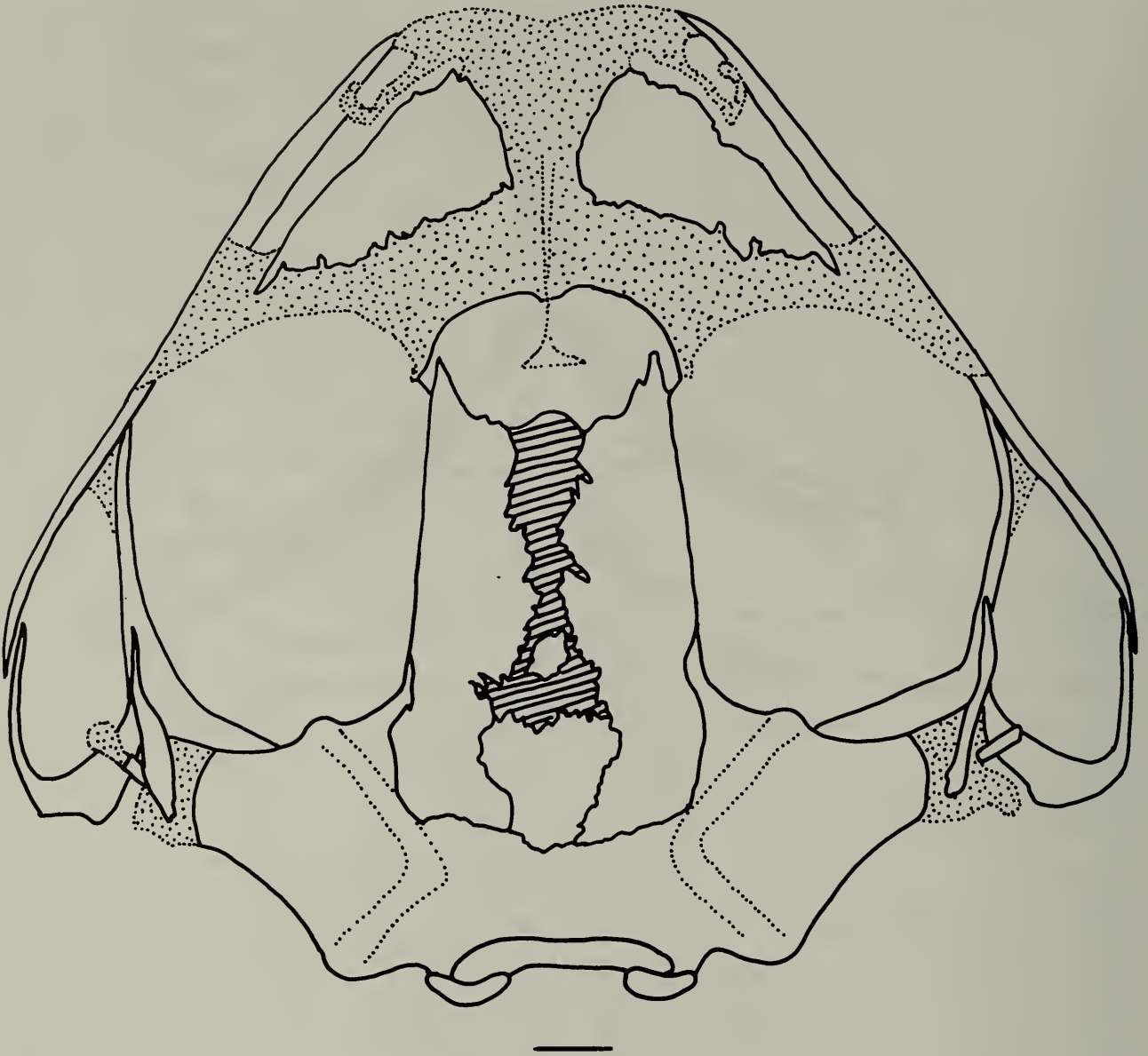


Fig. 3. Dorsal view of skull of *Rupirana cardosoi*, MZUSP 68959. Cartilage stippled. Frontoparietal fontanelle hatched. Scale line = 1 mm.

initiation of the subfamily. In the Bahia frog, the sacral diapophyses are flattened (not rounded), but they are not really enlarged (Fig. 1). However, the differences involved in the shape of the sacral diapophyses are minor and alone do not argue for a distinct tribe status for the Bahia frog.

Lynch (1971) included four genera in his concept of Alsodini: *Batrachyla*, *Eupsophus*, *Hylorina*, and *Thoropa* (in 1978 he restricted the Tribe Batrachylini to the genera *Batrachyla* and *Thoropa*). Of these, the Bahia frog is most similar to *Thoropa*. *Eupsophus* and *Hylorina* have the type II cervical cotylar arrangement; the Bahia frog

has type I. The maxillary arch of *Batrachyla* is incomplete and the quadratojugal is absent; the maxillary arch of the Bahia frog is complete (Figs. 3–4).

Lynch (1971:129–130) defined the genus *Thoropa* by 31 characters (following his numbers): (4) cervical cotylar arrangement type I; (10) alary processes of premaxillae directed dorsally and slightly anteriorly, relatively narrow at base; (11) palatal shelf of premaxilla very narrow with elongate palatal process present [I could not find where Lynch defined what a palatal process of the maxilla was and I do not find such a structure for either *Thoropa* or the Bahia frog];

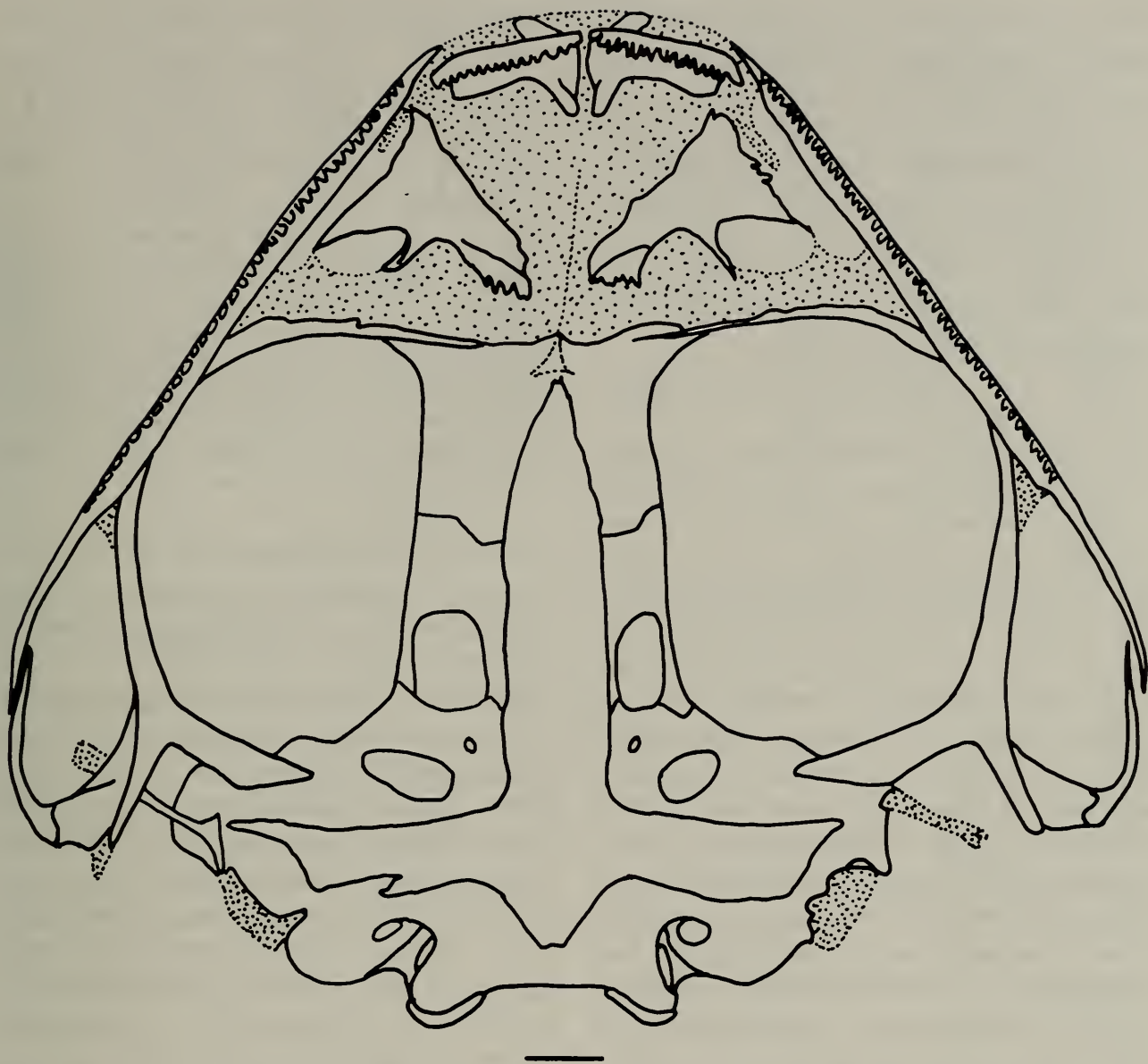


Fig. 4. Ventral view of skull of *Rupirana cardosoi*, MZUSP 68959. Cartilage stippled. Scale line = 1 mm.

(14) maxillary arch complete, quadratojugal present; (15) nasals relatively large with moderately long maxillary processes, separated medially; (16) nasals not in contact with maxillae or pterygoids; (22) epiotic eminences relatively long and narrow or short and stocky, carotid artery passes dorsal to skull bones; (24) zygomatic ramus of squamosal relatively short; (25) otic ramus of squamosal moderately long, no otic plate; (26) squamosal-maxillary angle 50–70°; (27) columella present; (28) prevomers relatively small, entire, separated medially, toothed; (29) palatine long and narrow, expanded laterally, separated medially; (30) sphenethmoid entire, extending anteriorly

to posterior edge of nasals or not reaching nasals; (31) anterior ramus of parasphenoid broad, keeled medially, extending anteriorly to prevomers; (32) parasphenoid alae oriented at right angles to anterior ramus of parasphenoid, relatively short, not overlapped laterally by median ramus of pterygoids; (33) pterygoids large, anterior rami in long contact with maxillae, not reaching palatines; (34) occipital condyles large or small, not stalked, moderately to widely separated medially; (36) terminal phalanges T-shaped; (40) *m. depressor mandibulae* in two slips; (41) pupil horizontal; (42) males with median subgular vocal sac; (43) body lacking glands; (44) tongue large, oval, pos-

terior edge free; (45) toes lacking webbing, bearing lateral fringes, digital tips bulbous, somewhat dilated, first finger shorter than second; (46) larvae with 2/3 tooth rows, labial papillae broadly interrupted anteriorly; (48) eggs large, few in number, laid in lotic situations; (49) males 19–78, females 24–70 mm SVL; (50) tympanum visible externally; (51) tadpoles with greatly flattened and attenuate bodies and tails.

There is no egg placement or larval information for the Bahia frog.

Several features require further comment. The Bahia frog does not have a medial keel of the parasphenoid, nor does the parasphenoid extend anteriorly to the vomers (Fig. 4), as stated for character 31 in *Thoropa*. However, Lynch's Fig. 86 (1971:130) does not show the conditions he described. In re-examining the material used by Lynch, I find that in *Thoropa miliaris* (KU 92855), the parasphenoid has a weak medial keel and does extend to the vomers, but in both *T. lutzi* (KU 92908), and *T. petropolitana* (KU 92862), the parasphenoid lacks a median keel and extends far short of the vomers (as in the Bahia frog). For character 32, in the Bahia frog the parasphenoid is overlapped by the median rami of the pterygoids, contrasting with Lynch's statement for *Thoropa*. However, Lynch's Fig. 86 (1971:130) shows overlap, which I also find in *T. lutzi* (KU 92908), *T. miliaris* (KU 92855), and *T. petropolitana* (KU 92862). The terminal phalanges of the Bahia frog, character 36, are not distinctly T-shaped as in *Thoropa*, but either expanded or weakly T-shaped (Fig. 5). Although the shape of the terminal phalanges in the Bahia frog differs from the distinct T-shaped condition in *Thoropa*, this condition could be interpreted as part of a morphological continuum in degree of expansion of the terminal phalanges. The depressor mandibulae muscle, character 40, of the Bahia frog is the DFSQat condition (three slips, the third a small slip originating from the tympanic annulus), contrasting with the DFSQ state listed for *Thoropa* by Lynch. I find

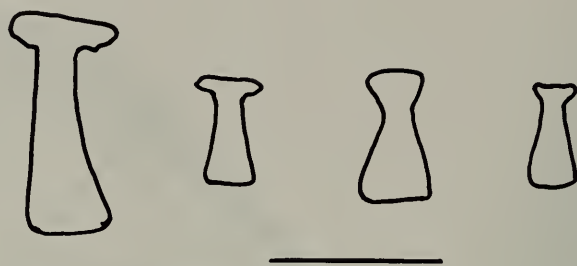


Fig. 5. Terminal finger phalanges. Left to right, *Thoropa lutzi*, from cleared-and-stained specimen KU 92908, third finger; *Thoropa petropolitana*, from cleared-and-stained specimen KU 92862, third finger; *Rupirana cardosoi*, from cleared-and-stained specimen MZUSP 68959, third finger; *Rupirana cardosoi*, from partially dissected wet specimen MZUSP 76035, fourth finger. Scale line = 1 mm.

both the two and three slip conditions in *Thoropa*, however (*T. miliaris*, DFSQ [USNM 97765]; *T. petropolitana*, DFSQat [USNM 164135]).

There have been two additional species of *Thoropa* described since Lynch's (1971) publication (*T. megatympanum*, *T. saxatilis*) which require modification of character 45 in that genus. *Thoropa lutzi* and *T. petropolitana* have weak lateral toe ridges that are less well-developed than in the Bahia frog. *Thoropa miliaris* has weak ridges, similar to the condition of the Bahia species. The toe ridges of *T. megatympanum* are even weaker than those of *T. lutzi* and *T. petropolitana*. *Thoropa saxatilis* lacks any toe ridge or fringe. The digital tips of the Bahia frog are narrow, not dilated. In both *T. lutzi* and *T. saxatilis*, the digit tips are dilated and the finger tips are more dilated than the toe tips. In *T. miliaris*, the digital tips are bulbous and somewhat dilated (Lynch's description), and there is no size difference between the finger and toe tips. In both *T. megatympanum* and *T. petropolitana*, the tips of the digits are slightly dilated but not particularly bulbous and the finger and toe tips are equal sized. The first finger is the same length as the second in the Bahia species, the same condition that I find in *T. miliaris* (contra Lynch). The first finger is shorter than the second in *T. lutzi*, *T. petropolitana*, and *T. saxatilis*. In *T. megatympanum*, the first finger is either just

shorter than the second or the first and second are of equal length.

Summarizing thus far, the Bahia frog is most similar to species in the genus *Thoropa*, but differs consistently by two characters used by Lynch (1971): shape of the terminal phalanges (but see discussion of character 36 above) and dilation of digit tips.

In a preliminary analysis of relationships of leptodactylid genera, I (Heyer 1975) came to quite a different conclusion from Lynch (1971) regarding the relationships of *Thoropa*. I did not recognize formal taxonomic groupings such as subfamilies and tribes, but used informal grouping names, which are equivalent in scope to Lynch's subfamilies. Specifically, my concept of a grypsine clade combined the content of Lynch's Grypsinae plus Elosiinae with the genera *Paratelmatobius* and *Thoropa*. The reasons for this very different viewpoint are due to two factors: although Lynch and I analyzed most of the same characters, there were some differences; and I attempted a phylogenetic analysis, whereas Lynch's analysis was phenetic.

I analyzed 37 characters. For the states that I listed for *Thoropa* (1975, table B, p. 51), the following differ from the conditions found in the Bahia species. Character 5, state B, disks on toes (see discussion of Lynch's character 45 above). Character 6, state A, no tarsal fold, flap, or tubercle. The Bahia frog has a tarsal fold, however, re-examination of *T. miliaris* indicates that specimens have weak tarsal folds as do specimens of *T. saxatilis*. Character 9, state D, toes with lateral fringe (see discussion of Lynch's character 45 above). Character 12, state B, depressor mandibulae origin from dorsal fascia, squamosal, and otic region only (see discussion of Lynch's character 40 above). Character 16, state B, omohyoideus insertion on hyoid body and fascia between posteromedial and posterolateral processes. In the Bahia species, the omohyoideus inserts only on the hyoid plate. Character 17, state B, iliocostalis externus ex-

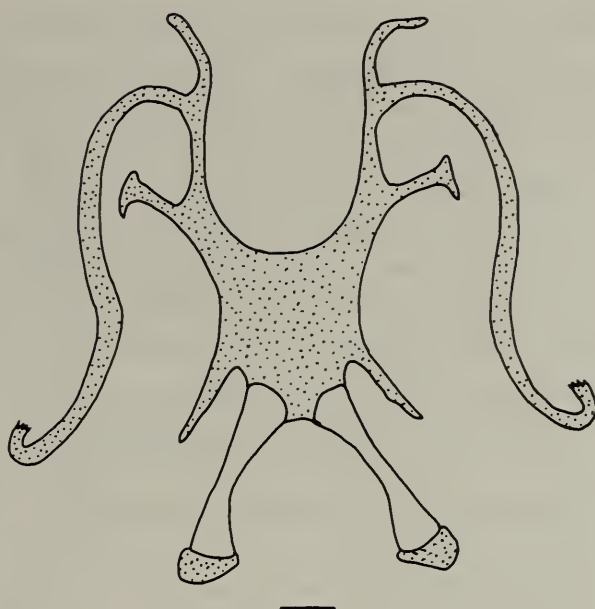


Fig. 6. Hyoid apparatus of *Rupirana cardosoi*, MZUSP 68959. Cartilage stippled. Scale line = 1 mm.

tends $\frac{1}{2}$ – $\frac{3}{4}$ anterior on ilium. In the Bahia species, the extension is $>\frac{3}{4}$, about 90%. Character 20, state B, adductor longus poorly developed, inserting on adductor magnus, covered by sartorius. In the Bahia frog, the adductor longus is well-developed, inserting on the knee. Character 30, state C, anterior process of hyale absent. In re-examining material, I found that the process is clearly absent in *T. miliaris* (USNM 97765). In *T. petropolitana* (USNM 164135), there is a medial, but not an anterior swelling of the hyale at its most anterior extent, contrasting markedly with the well-developed anterior process found in the Bahia species (Fig. 6). Character 34, state A, sacral diapophyses expanded. In the Bahia frog, the sacral diapophyses are flattened, but not expanded (Fig. 1). In re-examining the two *Thoropa* species that are similar in size to the Bahia species (*T. lutzi*, KU 92908, *T. petropolitana*, KU 92862), the sacral diapophyses are flat, as in the Bahia species, and differ slightly from the Bahia species in being expanded. Character 35, state B, terminal phalanges T-shaped is the same as Lynch's character 36 (see discussion above).

The Bahia species clearly shares most features of all known leptodactylid genera

with the genus *Thoropa*. The question is whether the definition of *Thoropa* should be expanded to include the Bahia species, or whether the Bahia frog should be treated as a genus distinct from *Thoropa*.

The Bahia species differs from all known *Thoropa* in seven characters (of the characters examined for this study). For two of these, the definition of the genus *Thoropa* would only have to be slightly modified to incorporate the Bahia frog: degree of expansion of the flattened sacral diapophyses and shape of the terminal phalanges. The other five characters would require a more drastic redefinition of *Thoropa*: toe disks; insertion of the omohyoideus muscle; length of the iliacus externus muscle; development of the adductor longus muscle; anterior process of the hyale. These latter five characters demonstrate different conditions involving toe, hyoid, and thigh morphologies. These kinds of differences are consistent with the Bahia species being on a separate evolutionary track from *Thoropa*. Thus, if the Bahia form were described as a species of *Thoropa*, evolutionary relationships would be obscured (also see section on relationships, below). Therefore, in order to emphasize the evolutionary distinctiveness of the Bahia species, it is described as:

Rupirana, new genus
Figs. 1–6

Type-species.—*Rupirana cardosoi*, new species.

Diagnosis.—The only leptodactylid genera that share the combination of sternum cartilaginous, widely spaced cervical cotyles with two distinct articular surfaces, long transverse processes of posterior presacral vertebrae, flattened sacral diapophyses, and an exposed frontoparietal fontanelle are *Batrachyla*, *Thoropa*, and *Rupirana*. *Batrachyla* has an incomplete maxillary arch; in *Rupirana* the maxillary arch is complete. *Thoropa* has well-developed T-shaped terminal phalanges, dilated digit tips, and

lacks an anterior process of the hyale; *Rupirana* does not have well-developed T-shaped terminal phalanges, has narrow digital tips, and has an anterior process of the hyale.

Definition.—Pupil horizontal; tympanum distinct; vocal sac single, subgular, slightly expanded externally; male thumb with one extensive and one small patch of keratinized sandpaper-like asperities; body without well-defined glands; digital tips narrow, not dilated; tarsus with a tarsal fold; outer metatarsal tubercle small; inner metatarsal tubercle large, ovoid, not cornified; toes with lateral fringes, joined at base of toes.

Adductor mandibularis muscle condition adductor mandibulae posterior subexternus only; depressor mandibulae condition DFSQat; geniohyoideus muscle contiguous medially; anterior petrohyoideus insertion on lateral edge of alary process and hyoid plate; sternohyoideus muscle insertion entirely near edge of hyoid body; omohyoideus muscle insertion entirely on hyoid plate; iliacus externus muscle extending almost to anterior tip of ilium; tensor fasciae latae muscle insertion posterior to iliacus externus muscle on iliac bone; interior and exterior portions of semitendinosus muscle uniting in a common distal tendon distally, exterior portion larger than interior; adductor longus muscle about same size and shape as sartorius muscle, inserting on knee and adductor magnus.

Quadratojugal present, contacting maxilla; frontoparietals not meeting medially, exposing moderate-sized fontanelle; vomerine teeth present; occipital condyles widely separated; anterior process of hyale present; alary processes of hyale on narrow stalks; posterior sternum a cartilaginous plate, terminally expanded and bifid; last presacral vertebra just narrower than sacrum; sacral diapophyses flattened, not noticeably expanded; dorsal crest of ilium present; terminal phalanges barely expanded, not or weakly T-shaped.

Etymology.—From the Latin *rupes*, rock, and *rana*, frog. The gender is feminine. The



Fig. 7. Dorsal view of male paratype of *Rupirana cardosoi*, MZUSP 76032.

name is to highlight the association of this genus with the campos rupestres of Brazil.

Content.—Monotypic.

Rupirana cardosoi, new species

Figs. 7–8

Holotype.—MZUSP 65203, adult male, 27 Sep 1987, Mucujê, Bahia, Brazil, 13°00'S, 41°23'W, Miguel T. Rodrigues.

Paratopotypes.—MZUSP 65202 (adult male), 65204 (adult male), 65205 (juvenile), same data as holotype; MZUSP 68959 (cleared and stained adult female), 68960 (juvenile), 2 Oct 1990, Miguel T. Rodrigues.

Paratypes.—MZUSP 68961–68962 (adult females), Morro do Chapeu, Bahia,

Brazil, 3 Oct 1990, 11°33'S, 41°09'W, Miguel T. Rodrigues; MZUSP 76017–76018 (adult males), 76023–76030 (adult males), 76031 (adult female), 76032–76034 (adult males), 76035 (adult female, skull removed), 76036 (adult male), 76037 (juvenile male), 76038–76040 (adult males), USNM 519755–519757 (adult males), 519758 (adult female), Andaraí, Bahia, Brazil, 12°48'S, 41°20'W, 19–22 Nov 1968, Werner C. A. Bokermann, Francisco M. Oliveira, and B. D. Silva.

Diagnosis.—As for genus.

Description of holotype.—Snout round in profile and from above; nostrils anterolateral, near tip of snout; canthus rostralis indistinct; loreal obtuse; tympanum distinct,



Fig. 8. Profile of head of holotype of *Rupirana cardosoi*, MZUSP 65203.

rounded, about $\frac{1}{2}$ diameter of eye; supratympanic fold distinct from behind eye to shoulder, bordering tympanum dorsally; tongue elongate, triangular, with slight emargination on anterior edge; vomerine teeth in two small transverse patches in line with posterior borders of small, round choanae, vomerine tooth patches separated from each other by about width of single tooth patch; vocal slits elongate; vocal sac single, subgular, indicated externally by lateral skin folds/wrinkles; finger lengths $I \approx II \approx IV < III$; fingers free of web, very slight lateral ridges; tips of fingers rounded, not expanded; palmar tubercle ovoid, just smaller than ovoid thenar tubercle; subarticular tubercles moderately developed, slightly pungent; no supernumerary tubercles; accessory palmar tubercles present, two in line with each digit; thumb with extensive keratinized sandpaper-appearing asperity from penultimate phalanx to base of thumb, a second ovoid patch on inner half of thenar tubercle; forearm slightly hypertrophied; dorsum, including upper eyelid, smooth with many scattered large white tubercles; body lacking any obvious glands; venter smooth except for areolate posteroventral thigh surfaces; belly disk weakly

indicated; toe lengths $I < II < V < III < IV$; tips of toes rounded, not expanded; toes with weak lateral ridges expanded into weak fringes at base of inner sides of toes II and III resulting in trace of strap-shaped basal web between toes I, II, and III; inner metatarsal tubercle small, round, about $\frac{1}{3}$ size of small, ovoid outer metatarsal tubercle; distinct but relatively weak tarsal fold extending about $\frac{1}{2}$ length of tarsus; sole of foot smooth; subarticular tubercles moderate, pungent.

SVL 27.3 mm; head length 9.8 mm, head width 10.3 mm; horizontal diameter of tympanum 2.1 mm, including annulus; distance from eye to posterior edge of naris 2.8 mm; internarial distance 2.5 mm; thigh length 12.5 mm; shank length 13.4 mm; foot length 14.3 mm.

In preservative, dorsal body brown with darker brown markings, upper limbs tan with brown markings; upper snout with a few irregular darker blotches and dots; irregular interorbital bar connecting with lichenous network behind eyes, rest of dorsum with mostly elongate blotches and broad stripes; upper limbs weakly cross-banded; distinct broad dark brown canthal stripe extending more faintly from nostril to

Table 1.—Measurements (mm) of adult *Rupirana cardosoi* from three localities in Bahia, Brazil.

	SVL		HL		HW		TD		E-N		IN		Thigh		Shank		Foot	
	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
Andaraí																		
Males (<i>n</i> = 20)	27.8	31.2	10.4	11.9	10.7	12.1	2.0	2.6	2.6	3.3	2.6	3.0	12.9	14.5	13.0	15.1	13.9	16.5
Females (<i>n</i> = 2)	30.2	34.4	10.4	11.8	10.3	12.3	2.0	2.6	3.0	3.1	2.8	2.9	13.1	14.3	14.0	15.1	14.9	15.6
Morro do Chapéu																		
Females (<i>n</i> = 2)	32.3	32.9	10.5	12.0	12.4	12.6	2.0	2.4	2.8	2.9	2.7	3.0	14.3	14.3	15.3	15.3	15.0	15.6
Mucujê																		
Males (<i>n</i> = 3)	27.3	27.6	9.8	10.3	10.3	10.6	2.1	2.2	2.7	2.8	2.3	2.5	12.5	12.7	13.4	14.0	14.1	14.3
Female (<i>n</i> = 1)	30.3		11.8		11.8		2.4		3.5		NA		13.5		13.9		14.4	

tip of snout (Fig. 8); upper lip mostly uniform light tan; supratympanic fold dark brown, expanded into dark triangular blotch posteriorly followed by series of small dark spots on anterior half of otherwise light tan flanks; throat, chest, and belly light tan with lighter spots lacking melanophores; sole of foot brown; posterior surfaces of thighs uniform tan.

Variation.—Available data do not indicate any marked variation in measurements among sites, with a suggestion of slight sexual dimorphism in size (Table 1). Measurement variation of the entire sample of adults (male *n* = 23, female *n* = 5) is (means in parentheses): SVL 27.3–31.2 (29.6) mm for males, 30.2–34.4 (32.0) mm for females; % head length/SVL 34–40 (37.3) for males, 32–39 (35.0) for females; % head width/SVL 36–40 (37.9) for males, 34–39 (37.0) for females; % tympanum diameter/SVL 7–9 (7.7) for males, 6–8 (7.2) for females; % eye-nostril distance/SVL 9–11 (10.0) for males, 9–12 (9.8) for females; % internarial distance/SVL 8–10 (9.1) for males, 8–10 (8.8) for females; % thigh length/SVL 44–48 (45.7) for males, 42–44 (43.2) for females; % shank length/SVL 44–51 (48.2) for males, 44–47 (45.8) for females; % foot length/SVL 47–54 (51.0) for males, 45–49 (47.0) for females. The sample size for females is small, but it does appear as though the female legs are proportionately shorter than in males.

The most striking variation in addition to the male secondary sexual characteristics involving vocal slits, vocal sacs, thumb asperities, and forearm hypertrophy is the sexual variation in dorsal texture. In females, the dorsum is either smooth or with a weak shagreen, whereas the males have many, large, white tubercles scattered profusely over the back (Fig. 9). In the specimens from Morro do Chapéu and Mucujê, the male dorsal tubercles are largely limited to the upper eyelids and the back. The males from Andaraí have a much more extensive distribution of tubercles, including the snout, outer arms, dorsal thigh surfaces,

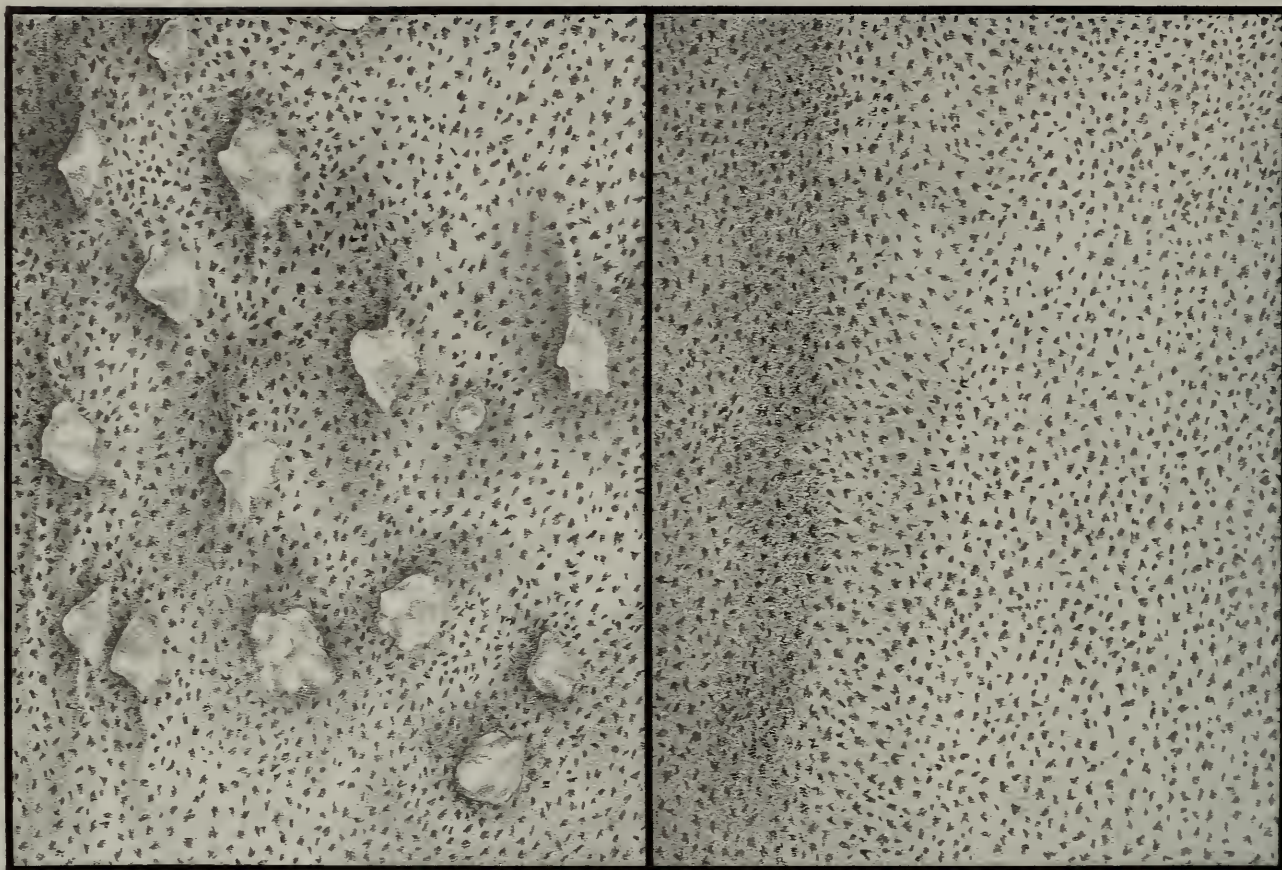


Fig. 9. Skin texture of male and female *Rupirana cardosoi*. Portions illustrated are at the transition from the dorsum to the flank above the arm insertion on the left side of the animal. Left illustration drawn from male specimen, MZUSP 76032, right illustration drawn from female specimen, MZUSP 76031.

dorsal shank surfaces, outer tarsus, and variably, the sole of the foot.

Other aspects of variation noted among the specimens (males and females, except as noted) include: tongue shape also ovoid or round; vomerine tooth placement between to just posterior to choanae, separated from each other by $< \frac{1}{2}$ distance of length of a single tooth patch; finger lengths also II just $< IV$ just $< I < III$; some males with no external indication of a vocal sac; finger subarticular tubercles sometimes pungent; outer tarsus sometimes shagreened; tarsal fold occasionally extending $\frac{2}{3}$ distance of tarsus; the inner metatarsal tubercle sometimes elevated; the sole of the foot sometimes with series of small, fleshy tubercles in line with digits; the dark supratympanic stripe sometimes extending continuously to mid-flank; front of tympanum sometimes bordered by dark brown spur extending from dark supratympanic stripe; dorsum relatively uniform to longitudinally

striped; chin through the chest sometimes scattered uniformly with melanophores with anterior belly with mottled pattern and posterior belly lacking melanophores to the entire region from chin through belly lightly brown mottled.

MZUSP 76037, a 29.4 mm SVL specimen, is a juvenile male, although not the smallest male in the sample. The specimen does not have vocal slits, but it has a small thumb patch asperity (on the thumb only, not on the thenar tubercle) and no dorsal tubercles. MZUSP 76039, a 30.2 mm SVL male, has vocal slits that are in early development, but has fully developed nuptial pads and dorsal tubercles.

The cleared-and-stained female (MZUSP 68959) contained mature-appearing ova, of varying sizes up to about 1.5 mm diameter with melanophores on the animal pole.

Etymology.—Named in honor of Dr. Adão José Cardoso, a colleague whose tragic death is deeply felt both at a personal

level and as a premature halt to his significant contributions to our understanding of the Neotropical amphibian fauna.

Distribution and habitat.—At present, *Rupirana cardosoi* is known from three localities in the northern portion of the Espinhaço Range in the State of Bahia, Brazil (Fig. 10).

Dr. Rodrigues kindly provided the following habitat information. MZUSP 65202–65205 were obtained during the day on the bank of a small stream with white sand and rocks. The stream crosses the city of Mucujê. The water of the stream was very clear but with a red-brown tint (as usual in the Espinhaço Range). The vegetation was typical of quartzitic campos rupestres: dominated by Velloziaceae, Euriocaullaceae, Xiridaceae and other endemics. There were many large and highly eroded quartzitic outcrops. MZUSP 68959–68960 were collected during the day at a similar stream habitat (2–3 m wide) less than 2 km from Mucujê. The general habitat was the same as for the Mucujê stream. Both of these sites were also visited at night, but no *Rupirana cardosoi* were found. MZUSP 68961–68962 were collected in a relictual patch of white sands on a large red rocky mountain not far from Morro de Chapéu. The frogs were on the margins of two small, drying ponds. The vegetation, dominated by Mellastomataceae on the sand, was typical for campos rupestres. Several specimens of the sand-adapted *Tropidurus cocorobensis* were also collected at the same time, around 1500 h.

Relationships

Rupirana shares the most character states with the genus *Thoropa*, as documented in the section, “Comparison with leptodactylid genera.” The evaluation of character states in that section did not differentiate between shared primitive and shared derived states, however. If most of the states shared by *Rupirana* and *Thoropa* are shared

primitive states, then there would be little support for a close sister-group relationship.

In order to undertake a first approximation of the relationships of *Rupirana* within leptodactylid frogs, the data assembled for an earlier study (Heyer 1975) are used as a basis for a cladistic analysis (Appendix 1). As indicated above, the relationships of *Thoropa* within the Leptodactylidae have been disputed by Lynch (1971, 1978) and me (Heyer 1975). In order to evaluate the relationships of *Rupirana* relative to *Thoropa*, the genus *Batrachyla* is included to evaluate Lynch’s position that *Batrachyla* and *Thoropa* are sister-taxa (Lynch 1978), and the genera *Cycloramphus* and *Megaelosia* are included to evaluate my position that *Thoropa* is a member of a grypiscine clade (Heyer 1975). Three additional representatives of telmatobiine genera are included to provide structure to test the alternative hypotheses: *Eleutherodactylus*, *Eupsophus*, and *Hylorina*. Three genera are used as outgroups: *Ceratophrys* as a representative of the South American ceratophryine clade and a representative each of two subfamilies of the Australian Family Myobatrachidae, *Adelotus* and *Crinia*. In all cases except for *Eleutherodactylus*, the character states analyzed are for genera. As *Eleutherodactylus* is currently in the process of being broken into smaller monophyletic units, with the final configuration of this effort far from clear, data for a single species, *E. coqui*, are used for purposes of this analysis.

The data were analyzed with as much ordering of character states as unambiguous morphoserries would allow (Appendix 1).

Phyletic signal in the data set.—The strength of the phyletic signal in the data set is evaluated with two tests: the indirect g_1 statistic (Hillis 1991) and the more direct Permutation Tail-Probabilities (PTP) test (Faith and Cranston 1991).

Hillis (1991) explained the rationale for the g_1 statistic and provided probability levels for cases using 6, 7, or 8 taxa. As there is no graphable correlation between the

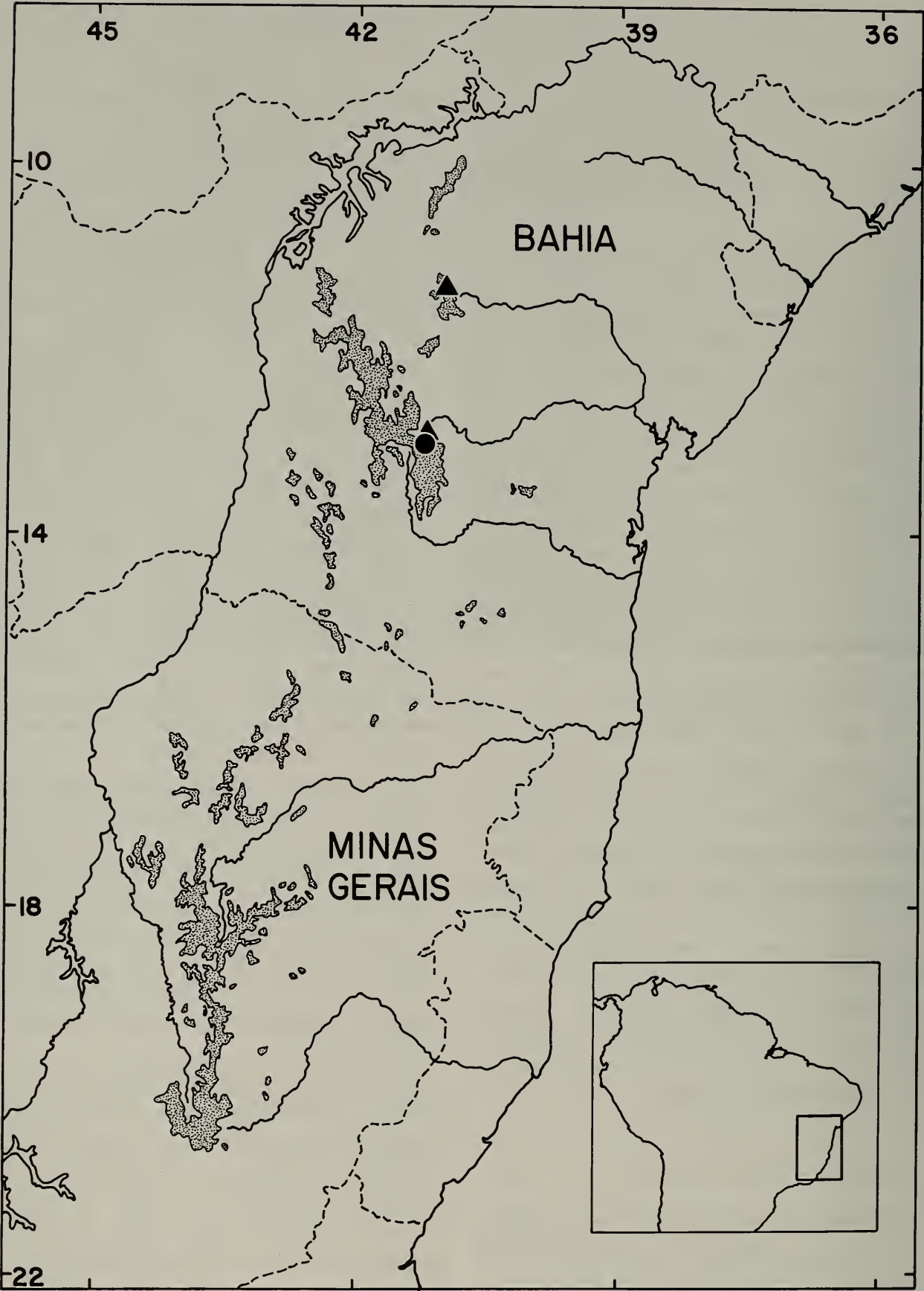


Fig. 10. The Espinhaço Range in the States of Bahia and Minas Gerais. Stippling indicates areas above 1000 m. Dot is the type locality of *Rupirana cardosoi*; triangles indicate the other two known localities for *R. cardosoi*. Map redrawn from Map 56, page 398 in Giuletti et al. 1997.

number of taxa and g_1 critical values, exhaustive PAUP analyses were run using 8 taxa with *Adelotus* or *Crinia* or *Ceratophrys* used as sole outgroup taxa and deleting *Hylorina*. The g_1 statistics for the 8 taxa are 0.31, 0.29, and 0.01 respectively when *Rupirana* is coded as not having T-shaped phalanges and 0.17, 0.39, and 0.08 respectively when *Rupirana* is coded as having T-shaped phalanges. The critical g_1 values for 8 taxa for P of 0.05 is -0.34 and P of 0.01 is -0.47 . None of the g_1 statistic values obtained in the six analyses approaches those critical values. The distribution of trees is not skewed.

The PTP test was run with *Rupirana* coded as not having T-shaped phalanges. The P value is 0.06, which is not significant at the traditional 0.05 level, but indicative that there is likely some phylogenetic content in the data.

Clearly, the phyletic signal in this data set is not strong and the results must be interpreted extremely conservatively.

Cladistic relationships.—The results of PAUP analyses run on the entire data set with a branch-and-bound search or with the outgroup taxa run individually with exhaustive searches (using the data matrix in Appendix 1) all have the same outcome: multiple numbers of shortest trees, for which the strict consensus tree is an entirely unresolved polytomy. The branch-and-bound search of the entire data set yields 19 shortest trees of tree length 112, with a consistency index (CI) excluding uninformative characters of 0.52. The exhaustive search of the data set using *Adelotus* as the sole outgroup taxon gives 240 shortest trees of tree length 86, with a CI value excluding uninformative characters of 0.56. Similar results for *Crinia* as the outgroup are 45 trees of length of 91, CI = 0.54 and for *Ceratophrys* as the outgroup are 45 trees of length 89, CI = 0.56.

In case the coding of the shape of the terminal phalanges in *Rupirana* might be pivotal, exhaustive searches were also run using *Adelotus*, *Crinia*, and *Ceratophrys* in-

dividually as outgroup taxa with *Rupirana* coded as having T-shaped terminal phalanges. Again the analyses resulted in multiple shortest trees with the strict consensus tree of each being an entirely unresolved polytomy. The results for using *Adelotus* as the outgroup are 240 trees of shortest length 85, CI (excluding uninformative characters) = 0.57; for *Crinia*, 150 trees of shortest length 91, CI = 0.55; for *Ceratophrys*, 45 trees of shortest length 88, CI = 0.56.

These results certainly do not resolve any questions about the relationships of *Thoropa* within the Family Leptodactylidae. However, there is one result that is so consistent that a statement about relationships can be made: *Rupirana* and *Thoropa* do not share a close relationship. In fact, *Rupirana* and *Thoropa* never form a sister-group relationship in any trees, and *Thoropa* either demonstrates a basal relationship with all or most other taxa or (usually) forms a sister-group relationship with *Batrachyla* (e.g., 17 out of 19 trees in the trees based on the entire data set). This *Batrachyla*-*Thoropa* sister-group relationship, repeated in most, but not all trees, lends support for Lynch's proposal of relationships. However, the potential problem of long-branch attraction (Swofford et al. 1996:427) would have to be ruled out to support the *Batrachyla*-*Thoropa* relationship.

The results of the above analyses indicate that the similarities analyzed between *Rupirana* and *Thoropa* are due to shared primitive state conditions, not shared derived states, and that there is no close sister-group relationship between the two genera.

Zoogeography

The campos rupestres contain a notably endemic biota at the species level (for a botanical introduction, see Giuletti & Pirani 1988), including amphibians and at least some reptiles (e.g., Vanzolini 1982, Rodrigues 1988). As I have extremely limited experience with the campos rupestres, the following comments are very superficial.

Hopefully these comments will encourage an honest zoogeographical study of the amphibians of the campos rupestres, because I think the amphibians show a pattern that differs from those based on study of other groups.

The campos rupestres occur above 800–900 m and, as the common name indicates, are rocky places with poor soils (see Giuletti & Pirani 1988 and Giuletti et al. 1997 for better characterizations and maps). Plants have been the most thoroughly studied campos rupestres group (Giuletti & Pirani 1988), otherwise, there has been little research on the distributions of other groups of organisms found in the campos rupestres with the exception of certain lizards (for *Tropidurus* see Rodrigues 1987, 1988, for other lizards see Vanzolini 1982). Most of the plant and lizard species found in the campos rupestres are either endemic to them or show their major central distributions on them. Species such as *Polychrus acutirostris* and *Tropidurus hispidus*, which occur in both the campos rupestres and more broadly beyond them, seem to be exceptional cases. Even though the endemism at the species level is rather astounding, there are few endemic genera of plants (Giuletti & Pirani 1988). The affinities for the campos rupestres endemic species are primarily with cerrado and caatinga species (for plants and *Tropidurus*), and cerrados and caatingas likely served as the primary source of species which differentiated in the campos rupestres environment. Whereas the campos rupestres could be considered a part of the diagonal of open formations (caatingas-cerrados-Gran Chaco), first noticed by K. P. Schmidt (e.g., Schmidt & Inger 1951), the campos rupestres do not fit comfortably within the diagonal from a zoogeographic perspective. Another common affinity for both plants and *Tropidurus* is with the restingas (sand beaches) scattered along the east coast of Brazil. In this case, the restinga associated elements are thought to be derived from campos rupestres ancestors (Giuletti & Pirani 1988, Rodrigues 1988).

The plants also show affinities that the campos rupestres lizards do not, i.e., with the mountain biotas of northern South America (stronger) and the Andes (weaker) (Giuletti & Pirani 1988, Harley 1988). There is a minor affinity with Atlantic Forest plants and lizards; the plant genus *Pleurostima* (Veliaceae) occurs on the tops of some granitic outcrops in the Atlantic Forests, and the Atlantic Forest lizard genera *Enyalius*, *Placosoma*, and perhaps *Heterodactylus* have representatives in the campos rupestres.

Most of our knowledge of campos rupestres amphibians comes from the work of Werner C. A. Bokermann and Ivan Sazima, who published several papers describing new species of amphibians from the Serra do Cipó, southern Espinhaço Range, in the State of Minas Gerais. Many of the new species described from Serra do Cipó belong to well delineated species groups or genera for which the general distributions are known. For most of these, the Serra do Cipó endemics are related to Atlantic Forest groups from which they must have been derived. For example all species of the genera *Hylodes*, *Phasmahyla*, and *Thoropa* and the *Scinax catherinae* species group occur only in the Atlantic Forests except for disjunct endemic species at Serra do Cipó (*H. otavioi*, *P. jandaia*, *T. megatympanum*, and *S. machadoi*). Determining the faunistic origin of several other species from the Serra do Cipó is not as clear, but it would seem that the majority of them were derived from Atlantic Forest lineages and a smaller number from cerrado groups. Some of the non-endemic species that occur at Serra do Cipó are likely cerrado species, such as *Leptodactylus furnarius*, *L. jolyi*, and *Physalaemus cuvieri*. Some of the Serra do Cipó endemics may also have been derived from cerrado ancestors, for example *Leptodactylus camaquara*, *L. cunicularius*, *Physalaemus evangelistai* and *Proceratophrys cururu*. The frog fauna of the campos rupestres thus has a strong faunal element derived from Atlantic Forest ancestors and

this pattern is different from that found in plants or lizards.

Remnants of the Atlantic Forest vegetation occur today in the Espinhaço Range (e.g., Pico das Almas, Harley 1995:20–24). The Atlantic Forests certainly were more extensive in the Espinhaço Range and continuous with the coastal forests during more mesic times. The campos rupestres, a very open formation habitat, would be expected to show biotic affinities with adjacent open formation habitats, as is true for plants and lizards. The campos rupestres would not be expected to show a primary affinity with the Atlantic Forest biota, as the basic adaptations for those two environments are profoundly different.

One aspect of anuran ecogeography could explain why many campos rupestres frogs were derived from the Atlantic Forest frog fauna rather than entirely from the cerrado/caatinga frog fauna. There are small streams (mostly seasonal at this stage of the interglacial) in the campos rupestres landscape. There are, as far as I know, no strictly stream-adapted frogs in the cerrados or caatingas, whereas many of the Atlantic Forest frogs are stream-adapted. Thus, the most probable source of stream frogs in the campos rupestres would come from the Atlantic Forests rather than the cerrados or caatingas. If, during periods of drier climates, the Atlantic Forests underwent gradual change, first contracting to gallery forests and then degrading to even more open vegetation, the stream frogs may have been able to adapt to the more open habitat conditions and occupy the campos rupestres.

In summary, from the available data, it would seem that the unique campos rupestres frog fauna has been derived from only two sources: Atlantic Forest (strongest); and cerrado/caatinga (the conclusion of Heyer 1988, that present data are inadequate to determine whether the caatingas harbor a frog fauna distinct from that of the cerrados is unfortunately still true).

The discovery of *Rupirana cardosoi* has one expected and one unusual zooge-

graphical consequence. The Espinhaço Range is comprised of a series of individual isolated mountains (Fig. 10), with many species narrowly endemic to single mountain systems within the entire Range (Giulietti & Pirani 1988). Finding a new species in the Chapada Diamantina, which is still poorly sampled for its frog fauna, is to be expected. What is unusual is that the new species also represents a new genus.

The fact that all but one of the endemic campos rupestres frogs are endemic only at the species level suggests that the differentiation of the campos rupestres biota occurred in a single episode and relatively recently in terms of geological time. Discovery of an endemic campos rupestres genus of frogs requires that the single episode of faunal differentiation requires emendment or explanation. There seem to be three most likely alternatives.

Rupirana is an endemic campos rupestres genus of frog. If this is true, that suggests that it had an earlier episode of differentiation than other campos rupestres endemic frogs. Although this alternative requires an additional episode of differentiation for frogs, this is not unusual for the rest of the campos rupestres biota, as there are endemic genera of campos rupestres plants (e.g., *Barbacenia* (Velloziaceae), *Morithamnus* (Compositae), *Pseudotrimezia* (Iridaceae), and *Raylea* (Sterculiaceae), Giulietti and Pirani 1988) and fishes (*Copionodon* and *Glaphryopoma* (Trichomycteridae), Pinna 1992).

Rupirana represents a sampling problem. It could be that *Rupirana* had or has a distribution with other species occurring in the Atlantic Forests (I think this more likely than in the cerrados/caatingas). If this is true, then either the Atlantic Forest species of the genus have become extinct and/or they are still extant but have not been found. The frog fauna of the northern Atlantic Forests is not well known and I would not be surprised if additional species of *Rupirana* were found there.

Recognition of *Rupirana* as a distinct ge-

nus is a taxonomic error. If this is the case, the new species does not require an historical zoogeographical explanation different from that for other campos rupestres endemic frogs.

Acknowledgments

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Figures 7, 8, and 9 were rendered by Rebekah St. John.

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Appendix 1.— Character state descriptions and data matrix for phylogenetic analysis of selected genera of leptodactylid frogs.

-
- Data from Heyer (1975) supplemented by taxa examined for this study as indicated in body of text.
 Multistate characters ordered by criterion of morphoserries when reasonable. Character states not polarized.
- Character 1. Pupil shape. State 0—round; State 1—horizontal.
- Character 2. Tympanum visibility. State 0—external, visible; State 1—partially concealed; State 2—concealed.
 Character state order 0-1-2.
- Character 3. Male thumb. State 0—no asperities; State 1—pad; State 2—spines. Character states not ordered.
- Character 4. Body glands. State 0—none; State 1—paratoids; State 2—inguinals. Character states not ordered.
- Character 5. Toe disks. State 0—none; State 1—disks but no grooves; State 2—disks with circumferential grooves; State 3—disks with dorsal scutes. Character states not ordered.
- Character 6. Tarsal decoration. State 0—none; State 1—fold; State 2—flap. Character state order 0-1-2.
- Character 7. Toe webbing. State 0—web; State 1—fringe; State 2—ridge; State 3—none. Character state order 0-1-2-3.
- Character 8. Life history. State 0—tadpole with $2/3$ denticle formula; State 1—tadpole with $>2/3$ denticle formula; State 2—tadpole with $<2/3$ denticle formula; State 3—direct development. Character states ordered in a triangular relationship with the following connections: 2-0-1; 2-3; 0-3; 1-3.
- Character 9. Depressor mandibulae muscle. State 0—three slips (DFSQAT to dfsqat); State 1—two slips (DFSQ to dfsq); State 2—one slip (SQ). Character state order 0-1-2.
- Character 10. Sternohyoideus muscle insertion. State 0—on lateral edge of hyoid plate; State 1—on lateral edge and midline of hyoid body; State 2—on midline of hyoid body. Character state order 0-1-2.
- Character 11. Omohyoideus muscle insertion. State 0—muscle absent; State 1—insertion on hyoid body and fascia between posteromedial and posterolateral processes; State 2—insertion on hyoid body only; State 3—insertion on hyoid body adjacent to posteromedial process. Character states unordered.
- Character 12. Iliacus externus muscle. State 0—extends $<1/2$ ilium length; State 1—extends $1/2$ – $3/4$ ilium length; State 2—extends $3/4$ –full length of ilium. Character state order 0-1-2.
- Character 13. Tensor fasciae latae muscle insertion. State 0—posterior to anterior extent of iliacus externus muscle; State 1—at same level as anterior extent of iliacus externus muscle.
- Character 14. Semitendinosus muscle. State 0—External head smaller than internal head, external head attached by tendon to internal head; State 1—as state 0, except internal and external heads displaced from each other; State 2—external head absent. Character states unordered.
- Character 15. Adductor longus muscle. State 0—well developed, insertion on or near knee; State 1—poorly developed, insertion on adductor magnus muscle; State 2—absent. Character state order 0-1-2.
- Character 16. Quadratojugal. State 0—present, contacting maxilla; State 1—absent.
- Character 17. Nasal contact with maxilla. State 0—present; State 1—absent.
- Character 18. Nasal contact with frontoparietal. State 0—absent; State 1—present, not fused; State 2—present, fused. Character states unordered.
- Character 19. Frontoparietal fontanelle exposed. State 0—not exposed; State 1—exposed.
- Character 20. Squamosal. State 0—zygomatic ramus about same length as otic ramus; State 1—otic ramus developed into plate; State 2—as State 1 and zygomatic ramus articulates with maxilla; State 3—otic ramus much smaller than zygomatic ramus, latter articulates with maxilla; State 4—otic ramus much larger than zygomatic ramus. Character states unordered.
- Character 21. Vomerine teeth. State 0—present; State 1—absent.
- Character 22. Median contact of vomers. State 0—absent; State 1—present.
- Character 23. Prootic fusion with frontoparietal. State 0—absent; State 1—present.
- Character 24. Occipital condyles. State 0—confluent; State 1—approximate; State 2—widely separated. Character state order 0-1-2.
- Character 25. Anterior process of hyale. State 0—present; State 1—absent.
- Character 26. Posterior sternum. State 0—cartilaginous plate, broadens posteriorly; State 1—cartilaginous plate, parallel or narrow; State 2—as State 1 with mesosternal mineralization; State 3—sternal style. Character state order 0-1-2-3.
- Character 27. Length of last presacral transverse processes relative to sacrum. State 0—about equal; State 1—last presacral processes $\ll$ sacrum.
- Character 28. Sacral diapophyses. State 0—expanded; State 1—rounded.
- Character 29. Terminal phalanges. State 0—simple, knobbed, or claw-shaped; State 1—T-shaped.
- Character 30. Iliac dorsal crest. State 0—absent; State 1—present.
- Character 31. Diploid number of karyotype. State 0—greater than or equal to 26; State 1—24.
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	Character																															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	
<i>Adelotus</i>	0	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	1	0	0	1	?	
<i>Crinia</i>	0	0&1&2	1	0	0	1	1&3	0	0&2	2	0	2	0	2	0	0	1	0	1	0	0&1	0	0	2	0	0	1	0	0	0	0	1
<i>Ceratophrys</i>	0	0&1&2	1	0	0	1	0	1	0	0	0	1	1	1	1	0	0	2	0	3	0	1	1	0	1	0	1	0	0	0	0	
<i>Batrachyla</i>	0	0	1	0	1	0	2	0	1	0	1	0&1	0	1	2	1	1	0	1	1	0	0	0	2	1	1	0	0	1	0	0	
<i>Cycloramphus</i>	0	2	0&2	2	0	0	0&2&3	0	1	0	1	1	0	1	0	0	0	1	0	1	0	1	0	2	1	1	1	0&1	0	1	0	
<i>Eleutherodactylus</i>	0	0	0	0	2	0	2	3	0	1	2	2	0	2	0	0	0	0	1	0	0	1	2	0	2	0	1	1	1	0	0	
<i>Eupsophus</i>	0	0&1&2	1	0	0	1	0&2	0	1	0	0&3	0&1	0&1	1	1	0	0	0	1	1	0&1	0	0	1	0&1	2	1	0	0	0	0&1	
<i>Hylorina</i>	1	0	1	3	0	?	1	2	?	?	?	?	?	?	?	1	0	0	1	1	0	1	0	1	?	?	0	0	?	?	0	
<i>Megaelosia</i>	0	0	0	0	3	2	1	0	1	0	1	1	0	0	1	0	0	0	0	4	0	0	0	1	1	2	0	1	1	1	0	
<i>Rupirana</i>	0	0	1	0	0	1	2	?	0	0	2	2	0	0	0	0	1	0	1	1	0	0	0	2	0	1	0	0	0	1	?	
<i>Thoropa</i>	0	0	1&2	0	1	0&1	0&2	0	0&1	0	1	1	0	0	1	0	1	0	1	1	0	0	0	2	1	1&3	0	0	1	1	0	